

BIOLOGY AND SYSTEMATICS OF THE
BEE GENUS *CRAWFORDAPIS*
(COLLETIDAE, DIPHAGLOSSINAE)

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Crawfordapis luctuosa (Smith) is a robust, dusky-haired bee, presently known from only a few localities in Mexico and Central America. Individuals can be as long as 24 mm and superficially resemble the more familiar diphaglossine bees of the genera *Ptiloglossa* and *Caupolicana* to which they are related. All three genera are placed in the Caupolicanini which is characterized by the complete pre-pisternal groove and very elongate first flagellar segment. While *Crawfordapis* is currently considered to be monotypic, Michener (1966) raised the possibility that the material from the more northern localities (Mexico and Guatemala) may represent a distinct species. Much more material from different localities is needed before that problem can be considered.

The purpose of this paper is to present biological observations made on *Crawfordapis* by three of us in Costa Rica (L.G., L.M., G.O.). In addition, the larva of *Crawfordapis* is described and the systematic interrelationships of diphaglossine genera are reviewed (R.M.).

BIOLOGY

Description of the Site

Two nesting aggregations of *Crawfordapis luctuosa* were observed approximately 5 km east of Monteverde, Province of Puntarenas, Costa Rica (10°18'N, 84°47'W) on trails at 1540 m elevation. The surrounding vegetation is best described as elfin forest, with some characteristic plant species being *Lycopodium cernuum*, *Senecio megaphyllus*, *Clibadium* sp., *Gunnera* sp. and *Myrica phanerodouta*

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(details in Lawton and Dryer, 1980). Frequent rains deposit approximately 3000 mm of precipitation annually on this area. Heavy mists augment this precipitation. Mean annual temperature is about 16°C (max = 27°C, min = 10°C) and during prolonged rainstorms, the temperature can remain at 15–16°C for 3–4 days. The wind generally blows 15 to 20 km/hr, but ranges from nearly calm to winds in excess of 100 km/hr during rainstorms (R. Lawton, pers. comm.).

Nesting aggregation No. 1 was directly on the Continental Divide, on a narrow ridge known as "La Ventana". The aggregation was first noticed in August 1975 and was still active but reduced in size to only 5 nests in February 1981. W. Guindon (pers. comm.) indicated the site was active as early as 1966. Bees apparently maintained nests in this area throughout the year (R. Lawton, pers. comm.). Nests were built in the lee of a slope which partially protected them from mist and rain (Fig. 1). In July 1977, there were 97 nests with tumuli in the approximately 18 m aggregation. The majority of the nests were within an elliptical area of about 8 m. Of the nests 29 were completely exposed in the trail, 50 were on nearly level ground and partially obscured by grasses and other herbs, and 18 were on the face of the sheltering embankment.

Nesting aggregation No. 2, located at the head of the valley on the road to Penas Bancas, was exposed to high winds and unprotected from rain (Fig. 2). In February 1978, the aggregation consisted of not more than 100–150 nests, but had enlarged to at least four hundred active nests by August 1978. Nests were found both on the edge of the road and down the adjacent steep, bare slope. By the last visit to the site in February 1981, the number of active nests had declined to 230. The adjacent slope had become covered with dense vegetation and lacked nests.

Description of the Nest

Entrances to active nests had tumuli approximately 7.5 cm in diameter and 4–7 cm in height (Fig. 3). The frequent rains obliterated tumuli of all nests except those in which bees were actively digging. Nest entrances consistently measured 1.0 cm in diameter. In each of three nests excavated in horizontal ground, the tunnel began nearly vertically for 7–14 cm and then continued downward at an angle of approximately 75°. In the diagrammed nest (Fig. 4)



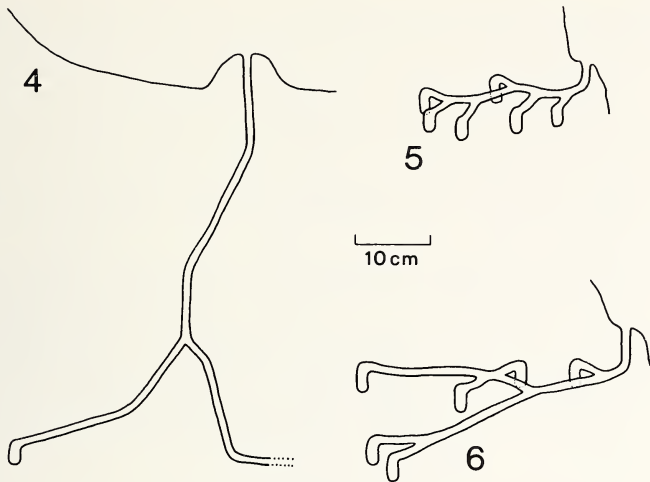
Figures 1-2. *Crawfordapis luctuosa* nesting sites. Fig. 1. Nest aggregation No. 1. Most nests were on level ground, either exposed or partially obscured by grasses. A smaller number of nests were in the nearly vertical embankment which sheltered the site from wind and mist. Fig. 2. Nest aggregation No. 2.



Figure 3. Nest tumulus. Nests in which bees were actively digging were readily discerned by the presence of a dirt mound around the nest entrance.

the tunnel changed directions again at a depth of 24 cm, continued downward at a 75° angle another 8 cm, and diverged into two tunnels. One of these angled toward the embankment at an angle of 50° from vertical for another 12 cm, then at a depth of 41 cm continued slightly below horizontal for another 18 cm. A single, terminal cell was found at the end of that tunnel. The other tunnel continued downward another 16 cm from the branching point before becoming nearly horizontal at a depth of 47 cm. This tunnel could not be followed because the soil was too soft.

Two additional nests were excavated on the nearly vertical embankment at aggregation No. 1. These nests differed from those in level ground in having very short (3–5 cm) vertical portions of the tunnel before becoming nearly horizontal. Nest B (Fig. 5) had a single horizontal tunnel that extended 22 cm into the embankment. Along the slight downward slope of this main tunnel were 6 nearly horizontal lateral tunnels 4–8 cm long. The two closest to the exterior contained pupae and the tunnels had been filled with soil. The next three contained larvae, and the distal cell was empty. Nest C



Figures 4-6. Diagrammatic representation of three *C. luctuosa* nests. Fig. 4. Nest at base of the embankment. Figs. 5-6. Nests excavated in the embankment.

(Fig. 6) had one cell (contents unrecorded) only 4 cm from the vertical entrance tunnel. Another 8 cm further down, the main tunnel diverged into two. One tunnel continued to slope downward and contained two terminal cells with pupae. The other tunnel sloped slightly upward and had two lateral cells with larvae and an empty terminal cell which was 34 cm from the face of the embankment.

Each completed cell was lined with a shiny, cellophane-like membrane which is characteristic of Colletidae. It was not possible to lift the cell and contents out of the soil as described for *Ptiloglossa guinnae* Roberts (Roberts, 1971). Cell contents were soupy; fermentation odors were not recorded. Cocoons were tough, nearly transparent membranes 17 mm in diameter by 35 mm in length.

General Activity Pattern

Females of *Crawfordapis luctuosa* were active aboveground primarily between the hours of 0930 and 1400 hr, with few bees leaving the nests after 1300 hr on observation days February 19 and 20, 1978 (Fig. 7). A similar activity pattern was recorded on July 16, 1977. This sharply contrasts with the crepuscular activity pattern of *Ptiloglossa guinnae* which occurs in similar habitats (Roberts, 1971). In some instances, bees were seen returning to the nests in the morning before any bees left the nesting aggregation. It is possible

that these bees had spent the night away from their nests as occurs with *Bombus* species at high elevations (O. R. Taylor, pers. comm.). Before leaving the nest for the first time in the morning, females often remained just below the nest entrance for a few moments and then upon exiting, hovered nearby for a short time before flying off. Temperatures within the nest entrance remained at 12°C throughout the day on February 20 when ambient temperature was between 10–11°C.

Males remained outside the nests at all times. During the activity period of the females, the males flew over the nesting aggregation and nearby at heights of 1–3 m. They rapidly approached any flying object, including female *C. luctuosa*, swallows, a hummingbird, a ctenuchid moth and a dragonfly. Males often seized females returning to the nests but it was not ascertained whether copulations occurred.

Nest Visitation Behavior

On February 19 and 20, 1978, 46 nests within a 2.16 m subarea of aggregation No. 2 were mapped and numbered. Sixteen female bees were captured while leaving nests. Each bee and her corresponding nest of origin were given an identifying color combination. The bees were marked by paint spots on the thorax, while their nests of origin were indicated by a wooden chip about 1 cm in length placed near the entrance. All observed departures from and arrivals to mapped nests were recorded by noting time, markings (or lack thereof) of bees and nest number or color. A nest "visit" was defined as the disappearance of the bee beneath the ground surface for any length of time.

Of the 46 nests mapped, 40 (80%) were entered at least once by a bee. The number of observed visits per nest made by marked or unmarked bees to the 16 color-coded nests ranged from 0–15 over the two days (Table 1).

Of the 16 marked bees, four were not observed again. The remaining 12 marked bees visited nests a total of 78 times. Four of the marked bees (BG, GO, YBY, OB) concentrated their visits on a single nest, while others entered up to 12 different nests over the two days (Table 2).

The duration of visits of both marked and unmarked bees varied widely from less than 1 minute to a maximum of 151 minutes. The

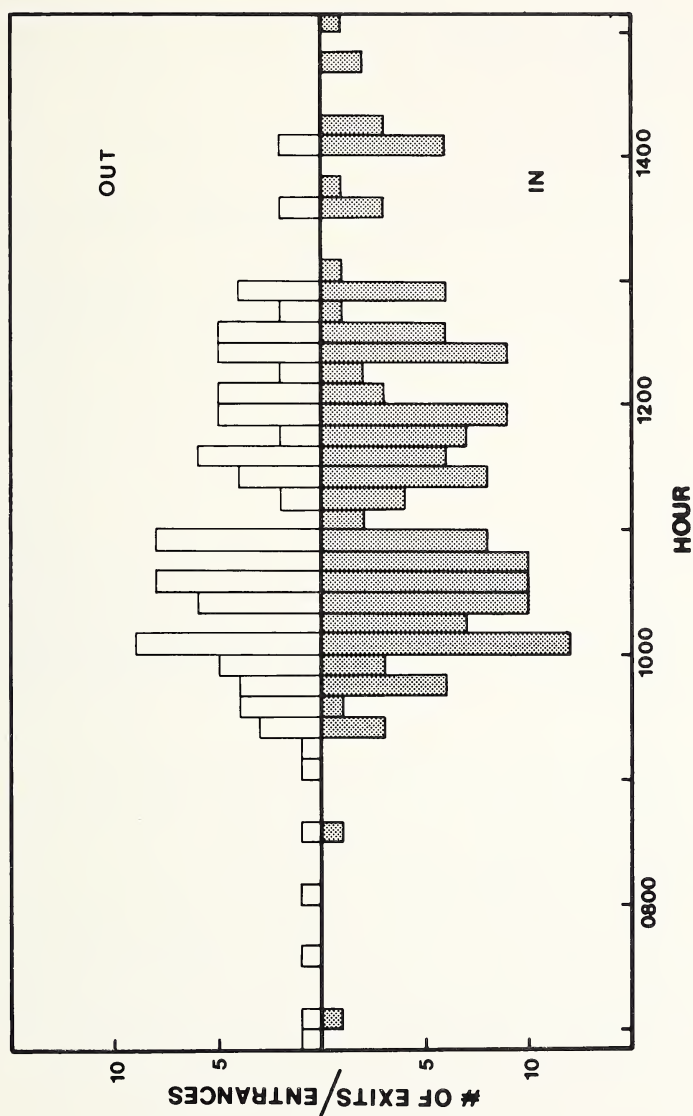


Figure 7. Number of bees exiting and entering nests in 10-minute intervals on February 19, 20, 1978.

Table 1. Number of visits by all bees to color-coded nests

	Nest Color-Code															
	YB	OY	YO	GO	BG	YBY	Y	OBO	O	OB	BY	YG	B	GB	OG	BOY
No. of visits	8	15	4	7	11	8	0	4	2	8	2	0	7	4	3	0

Table 2. Number of visits made by marked bees to particular nests.

Marked bee	Nest Categories												Total visits
	1°	2°	3°	4°	5°	6°	7°	8°	9°	10°	11°	12°	
YB	3	2	2	2	2	2	1*	1	1	1	1	1	19
OY	6*	4	2	1	1	1	1	1	1	1			19
YO	2*	2	2	1	1	1	1	1					11
GO	5	1	1	1	1								8
BG	5*												5
Y	1	1	1										3
YBY	3*												3
OB	3*												3
OBO	2												2
O	1	1											2
BY*,YG	Each visited one nest once.												

*Asterisked entries indicate that the visits were made to the nest from which the bee was originally captured.

visits of 1 minute or less were likely to have been exploratory rather than "working" visits. Of a total of 69 timed visits, 30 (43%) were in the "exploratory" category. The average duration of the remaining 39 "working" visits was 18.1 minutes ($S = 26.36$) (Fig. 8).

The duration of foraging trips of 4 of the marked bees was noted by timing of their absences from the nest area. Whether or not they returned with pollen was not noted. Absences ranged from 19–42 minutes, the average being 30.4 minutes ($n = 11$, $s = 13.79$). It seemed that bees returned from foraging trips in distinct pulses of several bees at a time. The foodplants are not known.

This preliminary data on the movements of marked bees to different nests generates several hypotheses for further testing.

- 1) Multiple nest entering is part of searching behavior for a female's own nest.

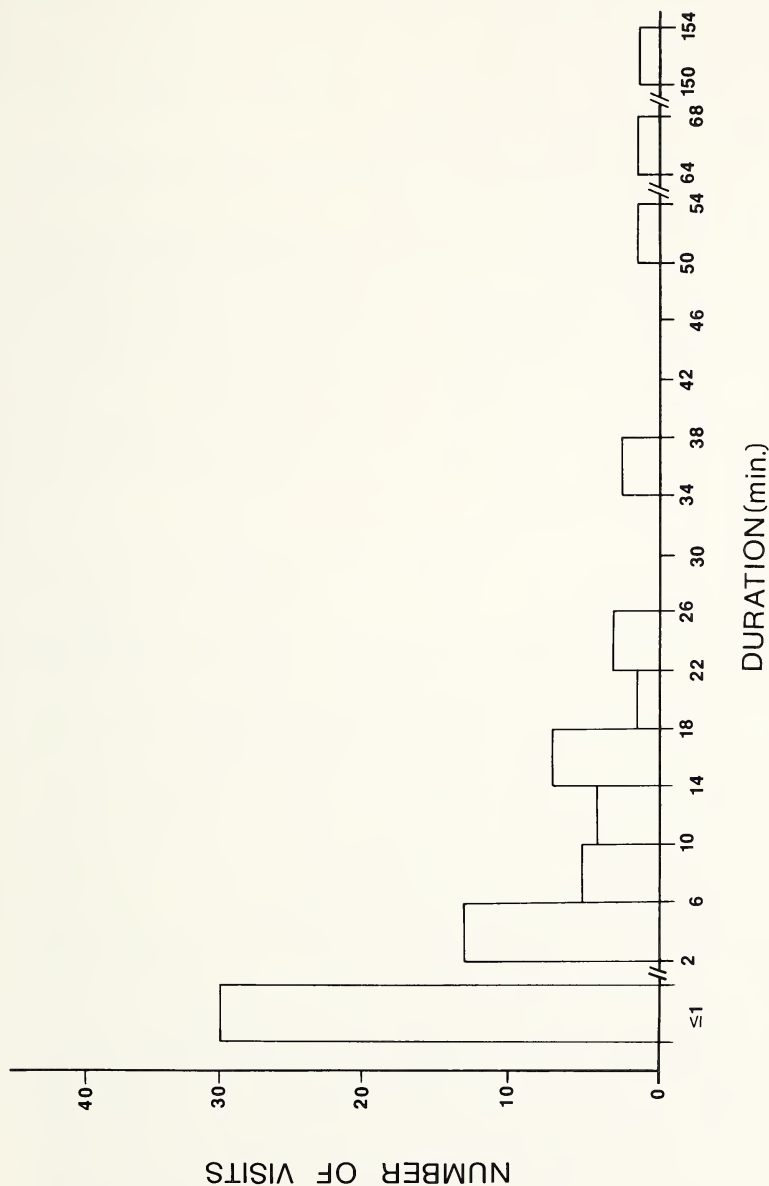


Figure 8. Number of visits by bees to nests as grouped in 4-minute intervals. The first category of visits of ≥ 1 minute may represent searching behavior and is set apart from the other categories.

- 2) Individuals are locating abandoned nests to provision rather than starting completely new ones.
- 3) Individuals are "stealing" provisions from nests of other individuals.
- 4) Individuals are usurping nests which other individuals are actively excavating or provisioning.
- 5) Several individuals are contributing to excavation, provisioning or oviposition within a single nest.

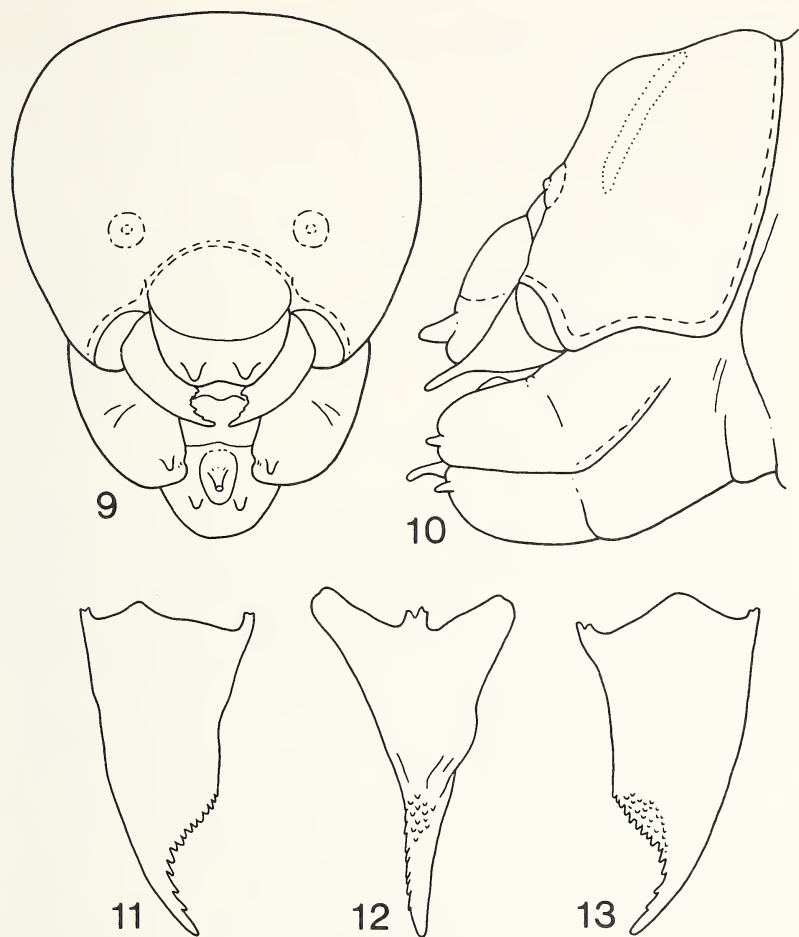
The latter hypothesis is particularly interesting since no species of the family Colletidae is known to be parasocial (Michener, 1974). It is plausible that females not only construct their own nests but also usurp partially constructed or provisioned nests of other females as has been reported in some other Hymenoptera that nest in aggregations (Brockmann and Dawkins, 1979; Brockmann *et al.*, 1979; Eickwort, 1975; Eickwort, 1981; Eickwort *et al.*, 1977). Further studies of *Crawfordapis luctuosa* are needed to better understand its social behavior and biology.

SYSTEMATICS

Description of Larva

The following description follows the format used for describing other colletid larvae (McGinley, 1981).

HEAD (Figs. 9–13): (2) Labrum nonspiculate; (3) epipharynx and (4) hypopharynx spiculate; (5) maxilla spiculate on inner surface. (7) Head size normal in comparison to body (head not relatively large as in Xeromelissinae); (8) head capsule somewhat elongate, slightly produced in lateral view; (10) frontal swellings above antennae absent; (10a) median frontal swelling above antennae absent (present only in *Ptiloglossa*). (14) Anterior tentorial pit low in position (high in all other known diploglossines); (15) posterior tentorial pit at junction of hypostomal ridge and posterior thickening of head capsule; (15a) tentorial development unknown (tentorium of specimen examined was incomplete, probably due to nearness of specimen to pupation). (16) Posterior thickening of head capsule moderately developed (17) straight medially, not curved forward; (19) median longitudinal thickening of head capsule absent; (20) hypostomal ridge well-developed; (25) epistomal ridge complete but thin, (26) arching dorsally to level of antennae. (27) Parietal bands distinct, broad and shallow. (28) Antennal prominence absent; (29)



Figures 9–13. Mature larva of *Crawfordapis luctuosa*. Figs. 9, 10. Head capsule, frontal and lateral view. Figs. 11–13. Right mandible, dorsal, adoral and ventral view.

antennal papilla a moderate-sized convexity, (31) bearing three sensilla. (32) Clypeus moderate in length; (34) labrum not projecting in lateral view; (35, 36, 37) labral tubercles very well-developed, narrowly rounded and strongly projecting (unlike those of other diphaglossines); (38) labral apex emarginate, (39) without sensilla-bearing swellings as in other diphaglossines. (41) Mandibles elon-

gate, (42) moderately slender in dorsal view, (43) broad basally in adoral view; (44) mandibular spiculation absent; (46) outer surface of mandible smooth, distinct tubercle and setae absent; (51) apical portion of mandible, in adoral view, attenuate; (52) cusp moderately well-defined; (53) cuspal projection absent; (54) cuspal region multi-dentate; (55, 55a) dorsal apical edge with distinct, moderately large teeth; (57) apical concavity weakly developed; (60, 60a) ventral apical edge smooth, teeth absent. (61) Labiomaxillary region produced; (62) labium and maxilla distinct, (63) subequal in length. (65) Inner apical surface of maxilla rounded, not produced mesiad; (66) unlike all other known bee larvae except those of *Ptiloglossa*, maxilla with a longitudinal groove on adoral surface; (67) cardo and stipes sclerotized; (69, 70) maxillary palpus moderately elongate and slender, (71) apically positioned on maxillary apex in lateral view; (72) galea absent. (73) Labium divided into prementum and postmentum; (75) palpus elongate and slightly decurved, (76) subequal to maxillary palpus in length. (77) Salivary lips well-developed; (78, 79, 80) salivary opening narrow, circular, at end of long spoutlike salivary lips, (83) which project from a well-defined platelike structure at apex of labium; (82) apical labial swellings absent. (84) Hypopharynx normal in size, (85) bilobed, (86) exceeded by labium and maxilla; (87) hypopharyngeal groove distinct, sclerotized laterally.

BODY (Fig. 14): (88) Integument spiculate, density of spicules greater on dorsum than on venter; (93) body moderate in length, (94) robust, (95) widest posteriorly in lateral view; (96) intersegmental lines moderately incised; (97) intrasegmental lines indistinct; (98) dorsal tubercles weakly developed, most prominent on abdominal segments 5-7; (103) lateral tubercles absent (present on one specimen from Panama); (104) ventrolateral tubercles absent; (106) abdominal segment 10 moderate in length, (107) rounded, (108) dorsal in attachment to segment 9; (109) venter of segment 10 slightly produced (very weakly so in specimen from Panama), (110) without conspicuous, darkly pigmented spiculation; (111) dorsal surface of segment 10 smooth, without lines or ridges; (113) anus apical. (114) Spiracles large, (115) not on elevations; (117) atrium very broad and shallow, (118) not produced above body surface; (119) atrial wall faintly ridged, (120) with four to five broken rings of spicules; (121) atrial rim absent; (122) peritreme wide; (123) primary tracheal collar absent; (126) subatrium apparently extremely

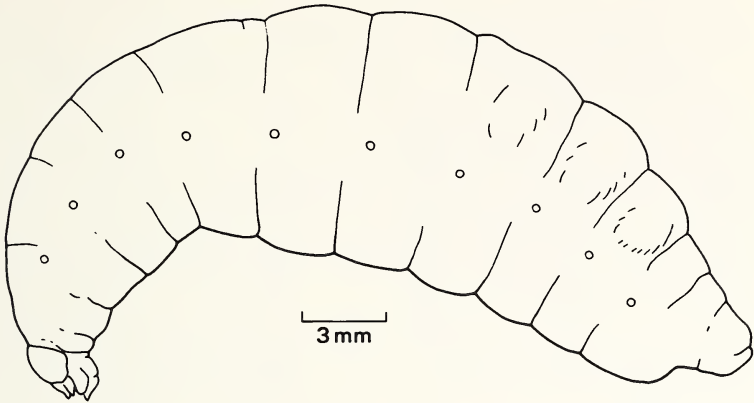


Figure 14. Mature larva of *Crawfordapis luctuosa*.

short. (The structure of diphaglossine larval spiracles remains poorly understood, especially with regard to the subatrium. The atrium is connected to the trachea by a long, nonringed tube. While this tube is characteristic of diphaglossines, its internal structure and homologies are not known.)

MATERIAL STUDIED: Two postdefecating larvae; 5 km east Monteverde, Puntarenas Province, Costa Rica; July 16, 1977 (G. W. Otis); specimens in the larval bee collection of the American Museum of Natural History. Two postdefecating larvae; Bouquete, Chiriqui Province, Panama; April 25, 1981 (R. W. Brooks); specimens in the personal collection of R. W. Brooks.

Analysis of Larval Characters

McGinley (1981) described the mature larvae of 30 colletid species including those of seven diphaglossines. Two cladograms for the diphaglossine genera appeared to be most strongly supported by larval characters. One of the cladograms, for reasons discussed in the above mentioned paper, appeared to be the preferable working hypothesis of diphaglossine phylogeny. This cladogram is presented in Figure 15, with *Crawfordapis* now included. The polarities of the characters listed in Table 3 were determined by out-group comparison, i.e., consideration of character state distributions in all other bee larvae as well as in nonapoid larvae, especially those of specoid wasps.

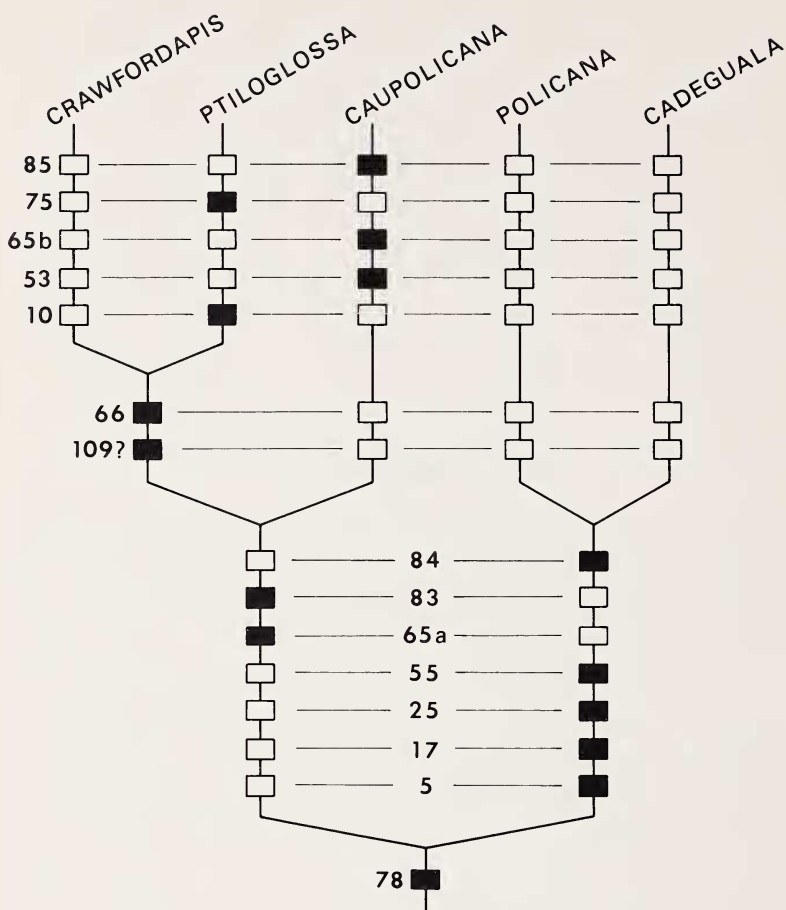


Figure 15. Cladogram of diphaglossine genera based on larval characters. Numbers refer to the characters listed in Table 3. Black rectangles represent presumed apomorphic characters; white rectangles represent plesiomorphic characters. Character 109 appears to be variable in *Crawfordapis*.

The larval cladogram corroborates the currently recognized diphaglossine classification based on adult characters (Michener, 1966). Recognition of the Caupolicanini (*Ptiloglossa*, *Crawfordapis*, *Caupolicana*) is supported by the presence of the unusual salivary plate (character 83, Fig. 9) and the rounded, nonprojecting inner maxillary surface (character 65).

Table 3. Larval Characters Used in Diphaglossine Cladogram

Plesiomorphic	Apomorphic
5. Maxilla spiculate	Nonspiculate
10. Median frontal swelling absent	Present
17. Median portion of posterior thickening of head capsule straight	Curved forward
25. Epistomal ridge complete	Incomplete
53. Cuspal region of mandible without distinct projection	Cuspal projection present
55. Teeth on dorsal apical edge of mandible distinct basally	Teeth fused basally, forming distinct platelike wedge
65. Inner apical surface of maxilla produced mesiad	a. Inner surface rounded b. Inner surface strongly produced forward
66. Inner surface of maxilla smooth	Inner surface of maxilla with longitudinal groove
75. Labial palpus moderately elongate, straight	Extremely elongate, decurved
78. Salivary lips transverse, not spoutlike	Elongate, spoutlike
83. Salivary plate absent	Present
84. Hypopharynx normal in size	Conspicuously narrow
85. Hypopharynx bilobed	Rounded
109. Venter of abdominal segment 10 not produced	Produced

The sister-group relationship of *Ptiloglossa* and *Crawfordapis* is strongly supported by the presence of a longitudinal groove on the inner maxillary surface (character 66). Weaker support for this relationship is indicated by character 109, the projection of the venter of abdominal segment 10 (this projection is conspicuous in some specimens of *Crawfordapis* but is only weakly developed in one specimen from Panama).

Adult Characters

In a study of adult diphaglossines, Michener (1966) discussed the similarities of *Crawfordapis* to *Ptiloglossa* and *Caupolicana*. Four characters found in *Crawfordapis* were said to be more or less *Caupolicana*-like: (4) outer hind tibial spur of male normal, articulated at base like inner spur; (6) lateral extremities of terga of male without areas of short, dense, erect hair; (7) sixth tergum of male with posterior margin not thickened or sulcate; (9) eighth sternum of male with apical process rather heavily pigmented, not down-curved. The similarity based on character 4 is definitely symplesiomorphic as the fusion of the hind tibial spur and the tibia is found only in *Ptiloglossa*. The other three characters appear to be plesiomorphic as well in that they represent the absence of some rather unusual features.

Similarities between adult *Crawfordapis* and *Ptiloglossa* appear to be apomorphic for diphaglossines: (1) clypeus strongly elevated above level of adjacent parts of face; (2) marginal cell prolonged basally as a narrow sinus to apex of stigma; (3) expanded second and third hind tarsal segments of female considerably expanded above. This evidence also supports the *Crawfordapis*-*Ptiloglossa* sister-group relationship indicated by larval characters, but must be considered tentative until a comprehensive cladistic analysis of adult colletids has been performed.

SUMMARY

Crawfordapis luctuosa, a large colletid bee, was studied at two nest aggregations in the mountains of Costa Rica. The aggregations were in exposed sites formed by landslides or clearing. Female bees slowly abandoned the aggregations as they became overgrown with vegetation. Several nests are described. In contrast to the crepuscular habits of the closely related genus *Ptiloglossa*, *Crawfordapis* was active primarily between 0930 and 1400 hrs. Some individually marked females showed a high degree of constancy in nest visitation, while others visited several nests in succession. The exact explanation of this behavior is not yet known. The previously unknown larvae of *Crawfordapis luctuosa* are described. Information from these larvae supports the placement of the genus in the

tribe Caupolicanini that was suggested from the systematic study of adults, and indicates that *Crawfordapis* may be the sister-group of *Ptiloglossa*.

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